DARWIN'S Madagascan Hawk Moth Prediction

BY GENE KRITSKY

It started on a quiet day in January 1862 with the arrival of a parcel addressed to Charles Darwin from Robert Bateman. The package contained several orchid specimens needed by Darwin for his research on insect pollination of orchids, including one that took Darwin by surprise. It was the "astounding" *Angraecum sesquipedale* Thouars, a large orchid with a nectary one foot long! Darwin thought, "what insect could suck it?" (Burkhardt & Smith 1985). And so began a forty-year story that illustrated the power of evolution by natural selection, created a controversy regarding creation, and predicted the existence of a "gigantic moth."

Angraecum sesquipedale is endemic to Madagascar. It possesses "large six-rayed flowers, like stars formed of snow-white wax . . . and a whip-like green nectary of astonishing length" (fig. 1) (Darwin 1862). Darwin measured several nectaries and

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found the average to be about eleven-and-a-half inches long. Because this group of orchids is moth pollinated, Darwin wrote in his 1862 book *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects*, "in Madagascar there must be moths with proboscises capable of extension to a length of between ten and eleven inches!" He did not know which family this hypothetical moth might belong to, but he speculated that the Sphingidae was the likely candidate.

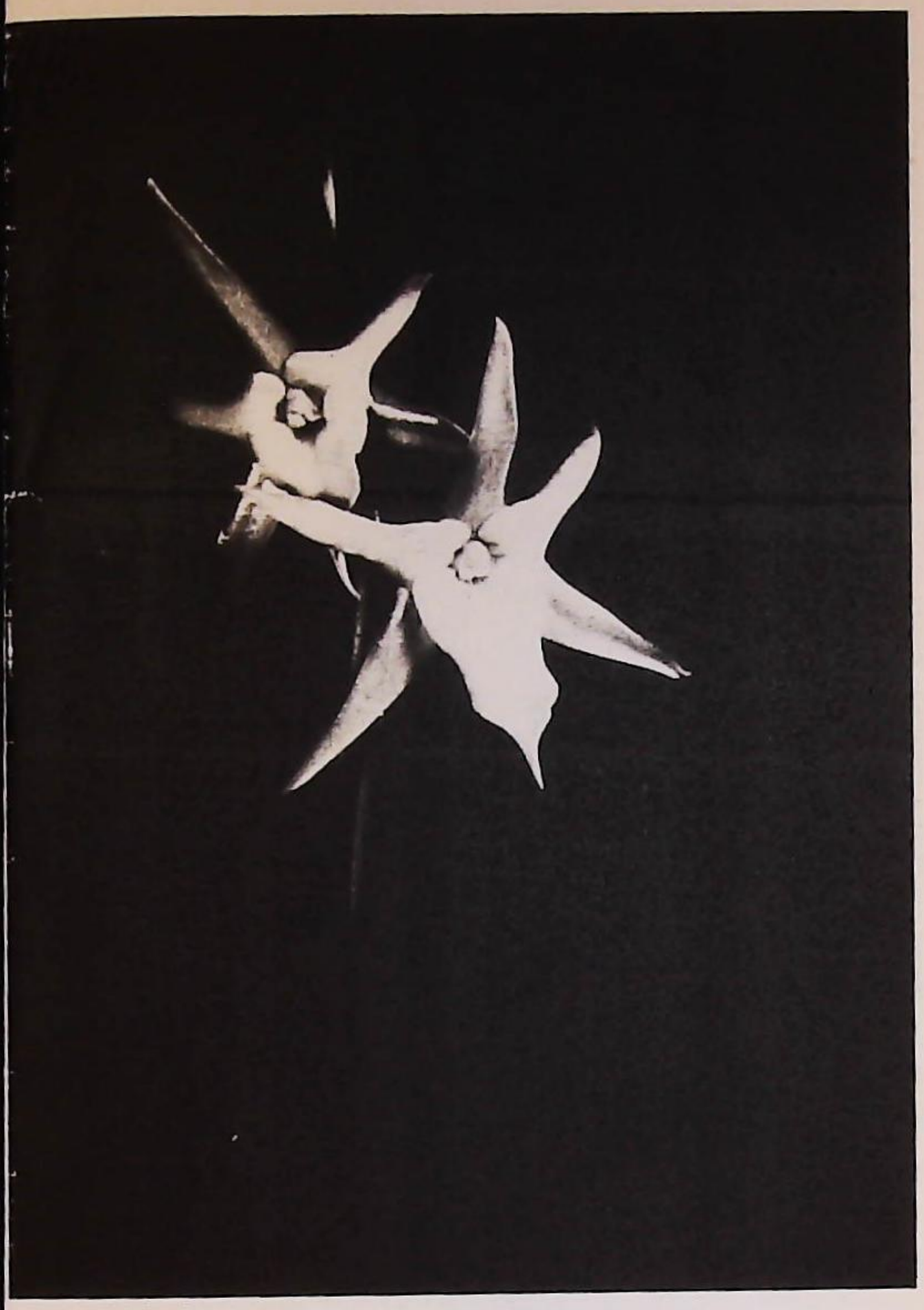

Fig. 1. Angraecum sesquipedale *with its long green nectary. Courtesy of Fred Hillerman.*

Darwin believed the long nectary was an adaptation to lure moths to the flower for pollination. He tested this hypothesis by imitating a moth's feeding process using a cylinder, which he probed into the nectary. When he removed the cylinder the orchid's pollinia adhered to the base of the cylinder. He then reinserted the cylinder into the nectary and was successful, although not every time, in causing the pollinia to be pushed onto the stigma (Darwin 1862). Darwin noted that nectar could be found only in the lower inch and a half of the nectary, thus requiring long haustellata to feed on the nectar. Small moths would not have proboscises long enough to reach the nectar and their actions would not cause the pollinia to be removed. This set up the selection pressure for the evolution of the moth–orchid complex. Orchids with nectaries, which forced large moths to insert their proboscises as far in as possible, would be pollinated more often and produce more seeds. This relationship was so specific, Darwin reasoned, that if the moth were to become extinct on Madagascar so too would the orchid (Darwin 1862).

Darwin's book on orchids delighted British readers. It provided a beautiful example of adaptation and helped explain how natural selection could be responsible for the adaptations seen in the orchids. But the Madagascan moth and *A. sesquipedale* complex also sparked controversy and was used as evidence of the existence of God by the Duke of Argyll in his 1867 book, *The Reign of Law*. The Duke (1873) examined British orchids and asked "How came this Orchis to require any exact adjustment between the length of its nectary and the proboscis of an insect? This is not a general necessity even among the Orchids. . . . We must start

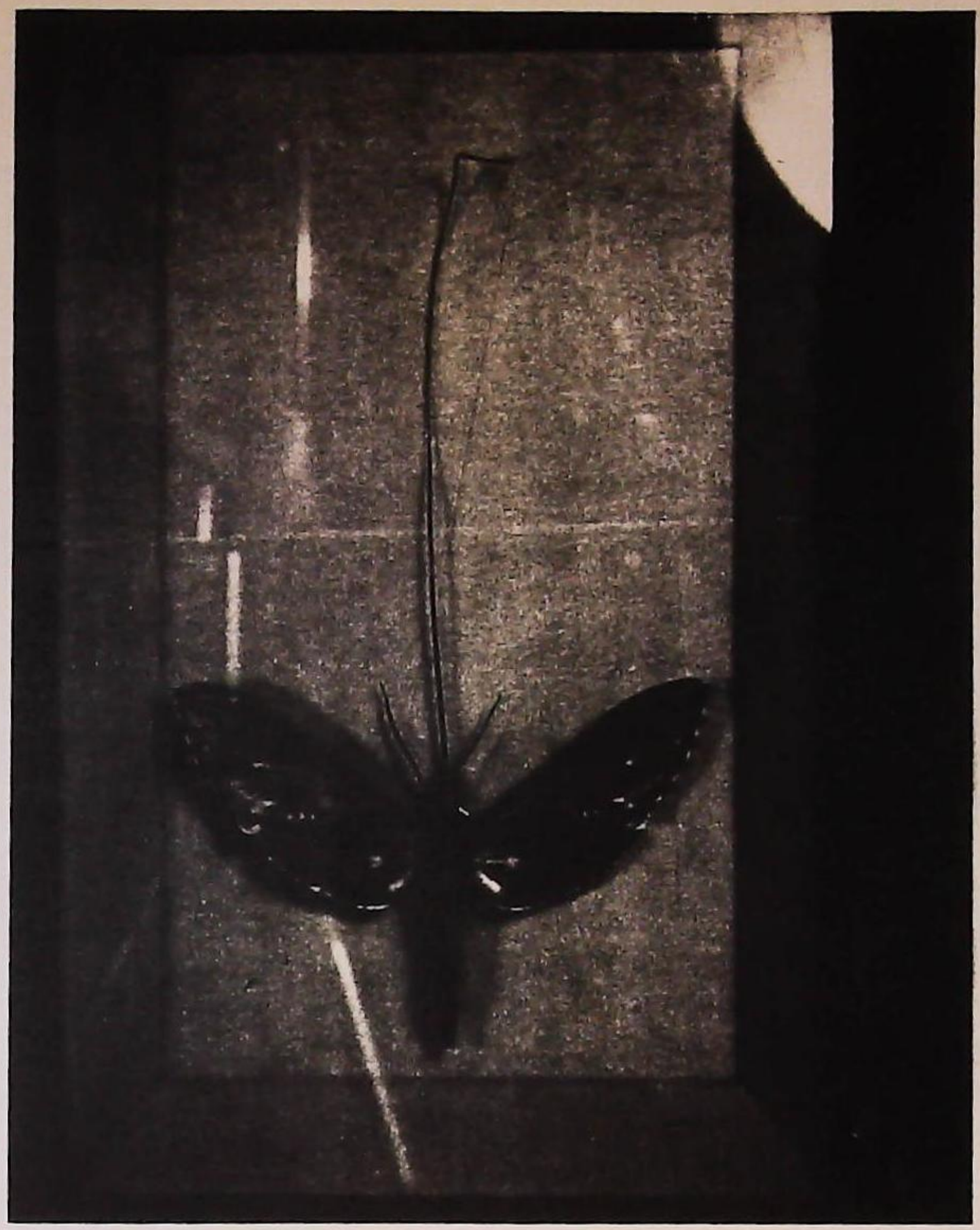

Fig. 2. Xanthopan morgani praedicta *with proboscis extended. Courtesy of Fred Hillerman.*

with this Madagascar Orchis already in possession of a larger nectary than other species, and with a structure already depending on particular moths also already existing, and already provided with proboscises of nicely adjusted lengths." The Duke believed that this moth–orchid relationship reflected "light of Reason and of Mind." And the mind in question was God's.

Darwin's colleague, Alfred Russel Wallace, decided to take on the Duke and responded in a paper titled "Creation by Law." Wallace (1867) detailed how a moth–orchid complex could evolve with only natural selection guiding the process. Wallace wrote, "Now let us start from the time when the nectary was only half its present length or about six inches, and was chiefly fertilized by a species of moth which appeared at the time of the plant's flowering, and whose proboscis was of the same length." Wallace argued that the orchids exhibited a variation in nectary length with some shorter and others longer. Those with the shorter nectaries were not pollinated because the moth did not have to struggle to get all of the nectar and therefore did not cause the pollinia to be transferred. On the other hand, the flowers with the longest nectaries would be pollinated most often because the moths with slightly shorter proboscises than the nectary would struggle to get the nectar from the bottom of the nectary and effectively cause the transfer of the pollinia. The moths with short proboscises would not get any nectar and would likely search for other aromatic flowers. But those moths that could reach the surface of the nectar would find a food source they would not have to share with many other moths. This open niche would favor the evolution of longer proboscises. As the moths' proboscises evolved to greater lengths, selection pressure on the

orchid to force the moth to struggle to get the nectar in order to insure pollination would favor the elongation of the nectary. Over time the orchid would develop a nectary that is on the average slightly longer than the average length of the moths' proboscises. Therefore, Wallace concluded, the moth–orchid complex did not demonstrate reason and a conscious creation but did exhibit the power of natural selection.

Wallace, like Darwin, believed that the moth would be found. He had measured the length of the proboscis of an African moth, *Macrosila morgani* Walker, and found it was seven-and-a-half inches long. Wallace (1867) wrote, "That such a moth exists in Madagascar may be safely predicted: and naturalists who visit that island should search for it with as much confidence as astronomers searched for the planet Neptune,—and they will be equally successful!"

In the 12 June 1873 issue of the journal *Nature*, W. A. Forbes challenged readers to find the moth. "Can any of your readers tell me whether moths of such a size are known to inhabit Madagascar?" Forbes' query was answered by Darwin's supporter Hermann Muller (1873) who did not know of any Madagascan moths with long proboscises but did report that his brother had caught a sphinx moth in Brazil with a proboscis nearly ten inches long. This meant to some that the prediction had been confirmed. Darwin's son, Francis, in a footnote in *More Letters of Charles Darwin*, wrote, "Mr. Forbes has given evidence to show that such an insect does exist in Madagascar" (Darwin & Seward 1903).

The motivation for Forbes' query to the readers of *Nature* is unknown. It apparently was taken as hostile by Darwin. Up to that time, entomologists were among the leading opponents of Darwin's evolution by natural selection. Indeed, he wrote to his friend, geologist Charles Lyell, "entomologists are enough to keep [evolution] back for half a century" (Kritsky 1981). In the second edition of his orchid book published four years after Forbes' letter, Darwin (1877) reiterated this moth prediction and added, "This belief of mine has been ridiculed by some entomologists."

The quest for the giant moth was realized in 1903 when Rothschild and Jordan described a large Madagascan sphinx moth (Rothschild & Jordan 1903). The new moth was a subspecies of the same moth that Wallace had examined and was appropriately named *Xanthopan morgani praedicta*. As expected, the moths are large with wingspans of about 150 mm and proboscises of about 300 mm (fig. 2). The moths have never been observed pollinating the orchid, because they are active at night and are apparently quite rare. However, the orchid has adapted to the scarcity of the moth by remaining open and attractive for weeks (Jolly et al. 1984).

The significance of this moth prediction goes beyond the historical details. It relates to Darwin's methodology and to his "evolution by natural selection." The scientific method dictates that hypotheses are tested by experimentation and that verified hypothesis takes on the status of a theory. Darwin's experimentation with *A. sesquipedale* pollination and the confirmation of his moth prediction is entomological verification of the theory of evolution via natural selection.

In recent years this episode in the history of entomology and evolution has taken an exciting turn. Another Madagascan orchid, *Angraecum longicalcar* Bosser, has been found with an even longer nectary than *A. sesquipedale*! This orchid's nectary is nearly 40 cm long, 10 cm longer than that of *A. sesquipedale* (Bosser 1965). The search can begin again. For somewhere in Madagascar is a gigantic moth with a proboscis even longer than Darwin's Madagascan hawk moth! ❑

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